

Consistent trade-offs in ecosystem services between land covers with different production intensities

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ABSTRACT

Sustaining multiple ecosystem services across a landscape requires an understanding of how consistently services are shaped by different categories of land uses. Yet, this understanding is generally constrained by the availability of fine-resolution data for multiple services across large areas and the spatial variability of land-use effects on services. We systematically surveyed published literature for New Zealand (1970–2015) to quantify the supply of 17 non-production services across 25 land covers (as a proxy for land use). We found a consistent trade-off in the services supplied by anthropogenic land covers with a high production intensity (e.g. cropping) *versus* those with extensive or no production. By contrast, forest cover was not associated with any distinct patterns of service supply. By drawing on existing research findings, we reveal complementarity and redundancy (potentially influencing resilience) in service supply from different land covers. This will guide practitioners in shaping land systems that sustainably support human well-being.

Key words: land-use planning, environmental management, ecosystem service bundles, quantitative review, network meta-analysis

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I. INTRODUCTION

Human transformation of the Earth's surface through land-use activities has reached an unprecedented magnitude, and constitutes a major driver of global environmental change (Turner, Lambin & Reenberg, 2008; Steffen *et al.*, 2015). Humans rely on resources appropriated through land use, however most of these practices affect the Earth's ecosystems in ways that undermine human well-being (Foley *et al.*, 2005). Continued population growth and increased *per capita* consumption of resources (Godfray *et al.*, 2010) make it critical to find ways to reconcile production and sustainability in land systems.

Ecosystem services (ESs) offer a framework for addressing these complex issues by explicitly accounting for the benefits that ecosystems bring to society. Central to this framework is the idea that human well-being is underpinned by a diverse constellation of ESs (MEA, 2005). Most of these ESs are not accounted for in conventional land-use planning and management decisions which, instead, tend to focus on the production of a single ES (e.g. provision of food or timber) (Robertson & Swinton, 2005; Rodríguez *et al.*, 2006). By highlighting the importance of multiple over individual services, the ESs framework encourages decision makers to prioritize long-term well-being over immediate economic reward (Costanza *et al.*, 2014; Guerry *et al.*, 2015).

As an additional layer, the ESs framework also links resilience in the delivery of ESs to resilience in human societies and the social–ecological systems in which societies participate (Sarkki *et al.*, 2017). Resilience in ES supply is supported by a combination of redundancy in the ecosystems (and their components, e.g. species) that supply the ESs and diversity in their responses to disturbances (Biggs *et al.*, 2012). Similar, but slightly differentiated, ecosystems and components within them are therefore necessary for resilient ES supply, and the spatial arrangement of these ecosystems may provide additional resilience through spatial averaging of service supply and dispersal of functionally important species (Loreau, Mouquet & Gonzalez, 2003).

Developing strategies that optimize ESs across different land uses, enhance multiple ESs within a single type of land use (Lambin & Meyfroidt, 2011), or ensure the resilient supply of ESs, relies on understanding the occurrence and interactions among different ESs and their responses to management interventions. To this end, important efforts have been made to map and quantify ES supply [see Crossman *et al.* (2013), de Groot *et al.* (2012) and Martínez-Harms & Balvanera (2012) for reviews] and, more specifically, to assess how different ESs are enhanced synergistically or traded off against each other (Nelson *et al.*, 2009; Bateman *et al.*, 2013).

More recently, research on ES trade-offs and synergies has come together under the concept of ES bundles: groups of ESs that repeatedly appear together in space and/or time (Raudsepp-Hearne, Peterson & Bennett, 2010; Saidi & Spray, 2018). Since ESs flow from the ecosystems that generate them to the human beneficiaries that enjoy them, ES bundles can be examined in terms of ES supply by

ecosystems (Queiroz *et al.*, 2015) and ES demand by human beneficiaries (Ament *et al.*, 2017). In either case, ES bundles can be used subsequently to identify common processes or external factors driving different ESs (Mouchet *et al.*, 2014).

Research on ES bundles has faced criticism on the grounds that spatial correlations or correlations between indicators of ESs are at times readily presented as evidence for interactions between services (Vallet *et al.*, 2018; Obiang Ndong, Therond & Cousin, 2020). This reflects a broader need for introducing a more mechanistic approach that can identify the drivers underpinning the relationships observed between ESs (Dade *et al.*, 2019). We do not attempt to duplicate those arguments here, but rather address the difficulties in obtaining cross-site comparisons and generalizations of bundles and their drivers. A systematic review of 51 studies on ES bundles linked those difficulties to the existence of multiple approaches to bundling ESs (Saidi & Spray, 2018). However, even when the same methods, data sets and groups of ESs were used to identify ES bundles and their relation to social–ecological variables in two regions, the results were highly inconsistent between regions (Spake *et al.*, 2017) and, therefore, not generalizable to other locations. This inconsistency may result from the choice of ES indicators, socio-ecological variables and spatial units of analysis (Spake *et al.*, 2017). Often, studies that examine ES bundles use administrative units (e.g. municipalities) as the scale at which ESs are quantified (Saidi & Spray, 2018). However, administrative units can mask ES associations because they: (i) are variable in size (within the same hierarchical level); (ii) occur at scales that are too coarse to capture the fine-scale processes linked to some ESs; (iii) encompass heterogeneous sets of land covers/land uses; and (iv) have boundaries that may cut across ecologically relevant units (Spake *et al.*, 2017). Therefore, identifying consistent rules regarding ES bundles and their drivers requires tailored analyses (Dade *et al.*, 2019) that focus on finer scales (Cord *et al.*, 2017), such as ESs measured in individual plots within land cover types (Spake *et al.*, 2017).

Here we test directly whether there are any general rules for the effect of land use on ES bundles by assessing the supply of multiple ESs across land covers (as a proxy for land use) at a national scale. We systematically surveyed the published literature for New Zealand (1970–2015) to collate studies with quantitative evidence of how different land covers compare against each other in processes relating to the supply of one or more ESs. For each study, we calculated standardized pairwise comparisons (expressed as log response ratios) of land covers in their supply of individual services. We used these ratios to conduct network meta-analyses for individual services and obtained, for each service, quantitative estimates of service supply from individual land covers.

With this comprehensive evidence base, we first discuss land cover effects on individual ESs and then examine associations between ESs to delineate any potential synergies and trade-offs arising from services that are best supplied by similar or different land covers. Similarly, we also examine associations between land covers based on the different ESs they supply. Previous research has shown that attributes of single

land-cover types can drive the value of multiple ESs (Sutherland, Gergel & Bennett, 2016) and trade-offs and synergies among ESs (Felipe-Lucia *et al.*, 2018). We therefore analyse patterns of covariance in the response of multiple ESs to land-cover differences in order to detect: (i) any land covers that may be operating as ‘generalists’ (i.e. supplying many ESs) or ‘specialists’ (i.e. supplying just a few ESs); and (ii) groups of land covers that supply similar profiles of ESs (i.e. ES bundles *sensu* Raudsepp-Hearne *et al.*, 2010). The latter includes services that are typically traded off against each other.

Duarte *et al.* (2018) present evidence that landscape composition metrics (e.g. percentage of natural areas and of non-crop areas) affect some ESs (water quality, pest regulation, pollination and disease mitigation); however, their analysis did not identify specific attributes of natural or non-crop areas that could shape ES supply. Therefore, as a second step we test whether there are generalities regarding how categories of land cover influence ES bundles (i.e. sets of ESs supplied consistently across more than one land cover) by testing for systematic differences between forested and non-forested habitats and between exotic-species-dominated production and native non-production land covers (note that we use the term ‘production’ to refer to economic activity rather than primary production). If they exist, these differences would suggest that production/no production, forest/non-forest cover and native/exotic vegetation are attributes that drive changes in ES supply across multiple land covers. By extending the perspectives of Duarte *et al.* (2018) to include attributes shared by multiple land covers, our results can potentially inform management decisions at broader scales and allow generalities across regions and land covers. We conclude with an example of how our findings can be used to examine the effects of land cover trajectories or contrasting management decisions on landscape-scale ES trade-offs.

II. METHODS

Unlike existing reviews and meta-analyses on ESs (e.g. Howe *et al.*, 2014; Nieto-Romero *et al.*, 2014; Malinga *et al.*, 2015; Lee & Lautenbach, 2016), our work does not collate existing ES assessments. Rather, we synthesize primary biophysical research that compares land covers in relation to a large variety of measures (which we term ‘ES indicators’) that indicate the supply of an ES, regardless of whether ES terminology was used. Therefore, the evidence base for our meta-analysis is not confined to the recent wave of studies focusing specifically on ESs, but also encompasses research that, having originated in a different field or during a time before ES terminology was widely used, still contains suitable data for quantifying ES supply across land covers. Our terms and criteria are described below in Section II.1.

Despite the growing literature on ESs (Chaudhary *et al.*, 2015), our understanding of ES bundles, trade-offs and synergies has traditionally been impaired by the lack of, and costliness of obtaining, detailed spatial data on

multiple ESs from multiple land uses across landscapes (Andrew *et al.*, 2015). This has led to the widespread approach of using expert or model estimates of ESs per land use or land cover class as input for ES assessments [see Jacobs *et al.* (2015) for a review; Aldana Domínguez *et al.* (2019) and Chen, Chi & Li (2019) provide recent examples]. Here, we propose an alternative approach that makes it possible to use primary data to study land cover and ES relations by capitalizing upon existing research across multiple disciplines.

We use New Zealand as a case study because the high levels of endemic flora and fauna and relatively recent introduction of large-scale intensive agriculture make conservation–production tensions particularly acute, and necessitate conservation strategies that go beyond protected areas (Craig *et al.*, 2000). Since human occupation began, the two main islands (North and South) of the New Zealand archipelago have lost an estimated 71% of their original indigenous forest cover (Ewers *et al.*, 2006). Although deforestation rates have decreased over recent decades and almost one-third of the country’s land area is protected as conservation land, the remaining forest may not be sufficient to prevent species extinction (Ewers *et al.*, 2006). Since 1960 the country has been experiencing accelerated intensification of its agricultural production, which is dominated by beef, sheep and, in the past two decades, dairy (MacLeod & Moller, 2006; Foote, Joy & Death, 2015).

Our systematic review was structured according to the *Guidelines for Systematic Review in Environmental Management* developed by the Collaboration for Environmental Evidence (CEE, 2013). We searched the literature for quantitative comparisons of two or more land covers in the supply of one or more ES within New Zealand. Our ES definitions were adapted from the Millennium Ecosystem Assessment (MEA, 2005), with a total of 32 ESs spanning the provisioning, regulating, cultural and supporting categories (see online Supporting Information, Supplementary Data Set S1). Despite debates on whether the MEA classification of ESs leads to double-counting of some services (Wallace, 2007; Fisher, Turner & Morling, 2009), we adopted it here because of its wide use and because our main interest was not to render a final valuation of ESs (where double-counting would be an issue), but instead to provide a comprehensive overview of the complete spectrum of direct and indirect benefits from ecosystems. Land uses, formally defined as the purposes to which humans put land into use (Dale *et al.*, 2000), were captured in our research as land covers (Supplementary Data Set S2), since these include units that are not directly used by humans and, consequently, correspond more closely with the actual experimental or sampling units of many of the documents in our search.

(1) Data collection, aggregation and calculation of effect sizes

Full details of the search and screening process are described in Supplementary Methods S1; here we present a brief

outline. We searched the *Scopus* database for titles, abstracts and key words with at least one match in each of the three components that structured our search: (i) 'New Zealand', (ii) land-cover and land-use terms, and (iii) ES terms (see Supplementary Methods S2 for the full search phrase). Land cover terms included all possible variations of 'land use' and 'land cover' as well as the names of specific land use and land cover types (both generic and specific to New Zealand). The ESs component drew upon the names of each service (and possible variations of these) but also included vocabulary describing processes and conditions that could reflect their supply at the site scale akin to individual land cover units. The search was finalized in January 2015, and was constrained to include documents published from 1970 onward, to be comparable with current land use regimes in New Zealand (MacLeod & Moller, 2006).

Our key word search yielded 9741 references. An initial automated screening process reduced these to 4373 publications by removing references that only mentioned a single type of land cover or land use in their title, abstract or key words. We excluded these studies because measures of ES supply from single land covers could not be standardized in a way that would make them comparable across studies and compatible with the standardized land cover comparisons of ES supply that informed the rest of our meta-analysis.

Publications with two or more land cover terms were scanned using Abstrackr, an interactive machine-learning system for semi-automated abstract screening, often used in medical meta-analyses (Wallace *et al.*, 2012). By learning from the abstracts or words that a user identifies as relevant during the screening process, Abstrackr can predict the likely relevance of unscreened abstracts and effectively assist in the exclusion of irrelevant ones (see Supplementary Methods S1 for further details).

Abstract screening yielded 914 relevant papers, which were passed on to a team of four reviewers for full-text assessment and data extraction. Studies that did not have replicated observations (as defined in Supplementary Methods S1) for any land covers were discarded, whereas studies that contained replication on some, but not all, of the land covers were retained, with only data on the replicated land covers extracted. Although we only included terrestrial land covers, ESs supplied by land but linked to a water body were included in our analysis. Full details of how the full-text selection criteria were applied can be found in Supplementary Methods S3. In total, we extracted data from 133 studies that met all inclusion criteria (see Supplementary Data Set S3 for bibliographic details of each study).

Information on the land covers, quantitative measures of ES supply, experimental design and bibliographic details for each study was collated in a database. To allow for comparability across studies, individual land covers described in each study were matched to the nearest category in New Zealand's Land Cover Database (LCDB; Thompson, Grüner & Gapare, 2003). This classification system includes forest, shrubland and grassland areas of either predominantly native or exotic vegetation, as well as cropland and

more artificial surfaces such as built-up surfaces and mining areas (Supplementary Data Set S2).

Often, the same quantitative measure of ES supply obtained from a study (indicators; provided in Supplementary Data Set S4) was relevant to more than one ES. This reflects the overlaps that exist between different ESs (e.g. soil structure plays a role in both soil formation and regulation of water timing and flows), and the multiple values that humans can receive from a given ecosystem process. We therefore decided to assign each indicator to as many ESs as it was relevant to, and use this allocation in our main analysis. However, to understand the influence on our results of sharing indicators among ESs, we also conducted the same analysis with each indicator assigned to only one ES. See Supplementary Results S5 for the results of this analysis.

For each indicator–ES combination, we defined the general direction of the relationship by determining whether larger values of the indicator would generally reflect an increase or decrease in ES supply. This was done because the majority of studies in our meta-analysis did not explicitly use ESs terminology. Instead, they measured environmental or ecological variables that could be used as indicators of ES supply, provided a conceptual link could be defined between the indicator (e.g. annual water discharge of a catchment) and the corresponding ES (in this case, provision of fresh water). When we could not readily assign indicators to ESs or determine the direction of the indicator–ES relationship, we consulted experts with specialized knowledge of the field related to each indicator (see Section VI). Although we recognize that the relationship between an indicator and an ES may be non-linear (e.g. pollination services may saturate with large numbers of pollinators; Fründ *et al.*, 2013), in most cases it was not possible to establish a clearly defined non-linear function, so we assumed a linear relationship for all indicators. The indicators we used to quantify ES supply are listed in Supplementary Data Set S4, which also provides an overview of the relations we defined between each indicator and ES.

Unique identifiers allowed us to define individual studies, regardless of whether they were within a publication that included more than one study or across different publications (Supplementary Methods S1). Multiple measures (i.e. pseudoreplicates) from within the same replicate site were aggregated into a single value per replicate (see Supplementary Methods S1 for details). Methods for standardizing measures of variance are presented in Supplementary Methods S4.

We obtained a final database with information on 457 ES indicators among 2943 pairwise comparisons of land covers from 133 studies. A log response ratio was used as the effect measure for comparing pairs of land covers within each study, and was standardized such that larger values always represented greater ES supply in the numerator land cover relative to the denominator one (see Supplementary Methods S1 for this standardization and log response ratio variance calculations).

Studies with more than one indicator of a given ES were aggregated to have the same weight as studies with only a

single indicator (this was based on either the mean log response ratio across multiple indicators or the single indicator represented in all land covers of a study, see Supplementary Methods S1 for details). Subsequently, the total number of land cover comparisons in our final data set of 133 studies was reduced from 2943 to 920 comparisons for individual ES within single studies (see Supplementary Data Set S5 for an overview of the final data set).

(2) Data analysis

Data analysis was conducted as a two-stage process: we first examined the supply of each ES by different land covers, and then assessed the relationships among land covers in terms of multiple ESs. For the first stage, we conducted a separate network meta-analysis (Salanti, 2012) for each ES. While conventional meta-analysis compares two treatments at a time (using direct comparisons from each study), a network meta-analysis can compare multiple (i.e. three or more) treatments simultaneously. This is achieved by using both direct evidence (studies comparing pairs of treatments) and indirect evidence derived from linking common treatments across different studies in a network of evidence (Salanti, 2012). For example, if some studies show that land cover A is better than B in supplying an ES, and others provide direct evidence that B is better than C, then a network meta-analysis allows us to make the indirect inference that A will also be better than C. We therefore used network meta-analysis to compare, for each ES, a wide array of land covers across different studies, even though we did not have data for direct comparisons among all combinations of land covers.

We conducted our network meta-analyses with the R package *Netmeta* (Schwarzer *et al.*, 2019), which offers a frequentist approach to calculate point estimates (and their corresponding 95% confidence intervals) of the effect of the different land covers on the supply of individual ESs. Estimates were expressed as the log response ratio of each land cover relative to a reference land cover: high-producing exotic grassland. We selected this land cover as our reference because it was the only land cover that was represented across all ESs in our data set (and would therefore allow us to compare our results across ESs at a later stage).

In *Netmeta*, we used a random-effects meta-analytic model to generate estimates and confidence intervals from which we then calculated probability scores (*P*-scores; Rucker & Schwarzer, 2015) on how different land covers ranked in the supply of each ES. Estimates, confidence intervals and *P*-scores then allowed us to construct, for each ES, a so-called forest plot or blobbogram (*sensu* Lewis & Clarke, 2001) to compare different land covers in their ES supply.

Bundles, trade-offs and synergies in land cover effects across the whole suite of ESs were then examined using hierarchical clustering of the network meta-analytic estimates. For this, we constructed a land cover by ES matrix (see Fig. S44, Supplementary Results S3) using the estimated log response ratios of each land cover (relative to the

high-producing exotic grassland reference) in each ES, as determined by the individual network meta-analyses. Missing values in this matrix resulted from sets of land covers for which we had no information on a given ES or could not infer the corresponding ratios indirectly.

For analysis, we selected subsets of this matrix with no gaps and the largest possible number of total cells. This resulted in two data subsets: a matrix of nine ESs by eight land covers and another matrix with nine land covers by eight ESs. The matrix with nine ESs was rotated to have ESs as rows (land covers as columns) and used to compare ESs in terms of the land covers that supply them. This allowed us to identify ES bundles (sets of ESs supplied similarly across multiple land covers), synergies in ES supply, and ESs that would likely be traded off with one another in land-use decisions. The matrix with nine land covers was used to compare land covers (to identify complementarity and redundancy) in the supply of eight ESs. This allowed us to explore how land-cover differences influence ES bundles.

We calculated a dissimilarity matrix from each of these matrices using the *daisy* function of the *cluster* package for R (Maechler *et al.*, 2019) with Euclidean distances. For the rotated matrix with nine ESs, distances were based on ES observations for each land cover, while for the matrix with nine land covers, distances were based on land cover observations for each ES. We applied hierarchical clustering (using the R *hclust* function; R Core Team, 2019) to each of the distance matrices and constructed dendrograms on how different land covers or ESs compared against each other. Following Raudsepp-Hearne *et al.* (2010), we also used these distance matrices to conduct k-means cluster analysis (with the *kmeans* function in the base package of R; R Core Team, 2019) to identify groups of land covers and ESs exhibiting similar behaviour. In each case, the number of clusters was determined using a scree plot (see Figs S3 and S4 in Supplementary Methods S5).

Finally, we used our distance matrices with nine land covers to test hypotheses on whether broad categories of land covers explained the trends observed in the corresponding clustering. Specifically, land covers were grouped under two categorical variables, one denoting the presence/absence of forest cover and another separating production land covers, dominated by exotic vegetation cover, from those with no production activities. Originally, we expected to compare land covers with a native *versus* exotic vegetation cover separately from production *versus* no production. However, we omitted the former category because, except for one, all land covers with exotic vegetation were production and all native covers had little or no production (see Table S1, Supplementary Methods S5). We used a permutational multivariate analysis of variance (PERMANOVA) to test whether these variables or their interaction explained between-land-cover differences in the supply of multiple ESs.

PERMANOVA analyses were conducted using the *adonis* function of the *vegan* package in R (Oksanen *et al.*, 2019). Variables are added sequentially in the *adonis* algorithm. To be conservative, we performed the PERMANOVA twice and

swapped the order of the variables in the second iteration, so that each variable was tested second, after controlling for any collinearity with the other predictor (i.e. adjusted sums of squares). The *betadisper* function of the *vegan* package was used to test the assumption of multivariate homogeneity of group dispersions, and all tests met this assumption. Table S1 presents the land cover categories used in these analyses.

III. RESULTS

(1) Data coverage

From our systematic survey, we identified a total of 133 studies that were relevant to our analysis and matched our selection criteria. Overall, these studies contributed data on 17 different ESs, 25 land cover types and 457 measures (which we term ‘ES indicators’) on ES supply. All four of the MEA ES categories (supporting, provisioning, regulating, and cultural services; MEA, 2005) were represented within our data set. However, most studies examined supporting and regulating services, with 115 and 110 studies, respectively. Only 44 studies presented data on provisioning services and four on cultural ones. All of the ESs in the supporting category (habitat provision, nutrient cycling, soil formation, water cycling and primary production) are represented in our database. Only four land cover comparisons had more than 20 studies (high-producing exotic grassland *versus* exotic forest, indigenous forest *versus* high-producing exotic grassland, short-rotation cropland *versus* high-producing exotic grassland and exotic forest *versus* indigenous forest); whereas the remaining land cover pairs were represented by 10 or fewer studies each. Further details on the number of studies per land cover comparison and per combination of ES and land cover are available in Supplementary Results S1.

(2) Land cover effects on individual ESs

There were consistent trends in the supply of multiple services by specific land cover types, but also great variability in the supply of some services. An overview of the evidence base (number of studies, types of ES indicators and network of land cover comparisons) and the outcomes of the individual network meta-analyses for each of the 17 ESs in our database is presented in Supplementary Results S2. In this supplement, we use forest plots (*sensu* Lewis & Clarke, 2001; see Fig. S8 in Supplementary Results S2 for an example) to show the main results of the meta-analysis, i.e. how different land covers compare against each other in their supply of individual ESs. Specifically, the values in these plots are given as log response ratios which express the overall estimates of service supply by individual land covers relative to a reference land cover (high-producing exotic grassland).

For several ESs, the positive log response ratio estimate and narrow confidence intervals in the forest plots (see Figs S8, S17, S19, S38, Supplementary Results S2) reveal that land

covers with native vegetation cover (broadleaved indigenous hardwoods, indigenous forest, tall tussock grassland and, in many cases, mānuka/kānuka) tended to rank higher in ES supply than the more intensive high-value production land covers (particularly short-rotation cropland and high-producing exotic grassland). Regulation of water timing and flows, water purification, freshwater provision and disease mitigation conformed to this general pattern. In these services, low-producing grasslands (which comprise a mix of exotic and native vegetation) and exotic forests also perform relatively well and, when present, always rank within the top half of all land covers.

For habitat provision (Fig. S13) the difference between land covers with native vegetation and production systems was less important than the presence of forest vegetation cover. For this service, most land covers with forest vegetation (exotic forest, broadleaved indigenous hardwoods and indigenous forest) ranked higher in their estimates of ES supply than those with open covers (short-rotation cropland, tussock, low- and high-producing grasslands) or deciduous hardwoods. Meanwhile, primary production (Fig. S23) tended to be highest under production systems (e.g. croplands, exotic forest, and high-producing exotic grassland) and lower in land covers with low or no production (e.g. low-producing and tall tussock grasslands, indigenous forest), rather than differing between forested and open covers. However, these trends were not statistically significant due to the wide and overlapping confidence intervals.

Importantly, these results indicate that no single land cover supplies all ESs at a maximal level. Indigenous forests ranked high in the supply of many ESs [particularly habitat provision (Fig. S13), freshwater provision (Fig. S17), disease mitigation (Fig. S38) and global climate regulation (Fig. S21)]. However, in some ESs they were outperformed by other land covers such as tall tussock grasslands (which were well suited to water purification; Fig. S19) and advanced successional forest (broadleaved indigenous hardwoods, which ranked high in regulation of water timing and flows, nutrient cycling and habitat provision; Figs. S8, S11 and S13). Therefore, multiple land covers will be required within the landscape to ensure the supply of multiple ESs.

The forest plots for primary production (Fig. S23), erosion control (Fig. S27), pest regulation (Fig. S30), waste treatment (Fig. S32), capture fisheries (Fig. S34), ethical & spiritual values (Fig. S36), pollination (Fig. S41) and regional & local climate regulation (Fig. S43) all present wide, overlapping confidence intervals for all or most of their estimates. This suggests statistically non-significant differences in the supply of these services among land covers. For some services, this could be due to small evidence bases, either in terms of few studies or few comparisons for specific land cover pairs within the network of land cover comparisons that inform the meta-analysis. However, in the case of erosion control, where the evidence base is formed by 22 studies (see Supplementary Results S2), overlapping confidence intervals in the land covers with the greatest number of comparisons (which would therefore be expected to have lower variance) still expressed high variability in ES supply, suggesting that other factors besides land cover (e.g. slope, soil type) likely account for the differences in erosion control across the sites in all 22 studies.

(3) Land cover effects across multiple ESs

We explored how the above trends in the supply of individual services translate into bundles, synergies and trade-offs among ESs. For this, we conducted multivariate analyses to simultaneously explore differences in the supply of multiple services across land covers (see Section II.2 and Fig. S44 in Supplementary Results S3). These analyses allowed us to examine whether groups of ESs responded similarly to differences in land cover and, conversely, whether groups of land covers played a similar role in the supply of multiple ESs.

(a) Differences among ESs based on the land covers that supply them

For this analysis we used a matrix of eight land covers by nine ESs to identify clusters of ESs based on how they are supplied by different land covers. We identified a total of five clusters, three of which were formed by only one ES while the remaining two had two and four ESs each (Fig. 1). This suggests that more than half of the nine ESs in this analysis are supplied in a distinct way by different land covers, and reinforces the notion that multiple land covers are required to supply a range of ESs. Moreover, the separation of services into clusters of one or two also suggests that their supply is traded-off across land covers. This trade-off is acute for water-related services; most of which tend to occupy distinct spaces within the dendrogram, with water cycling standing apart from all other ESs, water purification and freshwater provision in a separate cluster, and regulation of water timing and flows in a single branch close to global climate regulation and nutrient cycling (Fig. 1). Freshwater provision and water purification form a cluster because the water-quality aspect

of their supply was assessed with the same indicators for both services (Supplementary Data Set S4) and, in both cases, greater service supply came from land covers contributing to enhanced water quality (such as tall tussock grassland and indigenous forest; Figs S17 and S19).

In contrast to water-related ESs, those more closely linked to the soil system (nutrient cycling and soil formation) are found closer to each other in Fig. 1, and appear to be delivered similarly across land covers (Figs S11 and S15). In our analysis, global climate regulation falls under this broad group of services and is closely linked to nutrient cycling (Fig. 1).

(b) Differences among land covers in their supply of services

Our analysis of how land covers compared against each other in their supply of ESs was based on a matrix of nine land covers by eight ESs. We found a gradient of land covers that separates those with lower production from high-value production systems (Fig. 2). Land covers with high production value and dominated by exotic vegetation cover (croplands, high-producing exotic grassland, exotic and harvested forests) occupied separate clusters from those with low or no production and primarily native components in their vegetation cover (tall tussock and low-producing grassland, mānuka and/or kānuka and indigenous forest). Likewise, with the exception of low-producing grassland, land covers with forest vegetation cover occupied separate clusters from those with a more open vegetation cover.

The clusters with single land covers in Fig. 2 appear to specialize in supplying high levels of only one to three of the nine ESs used in the analysis. Tall tussock grassland supplies high

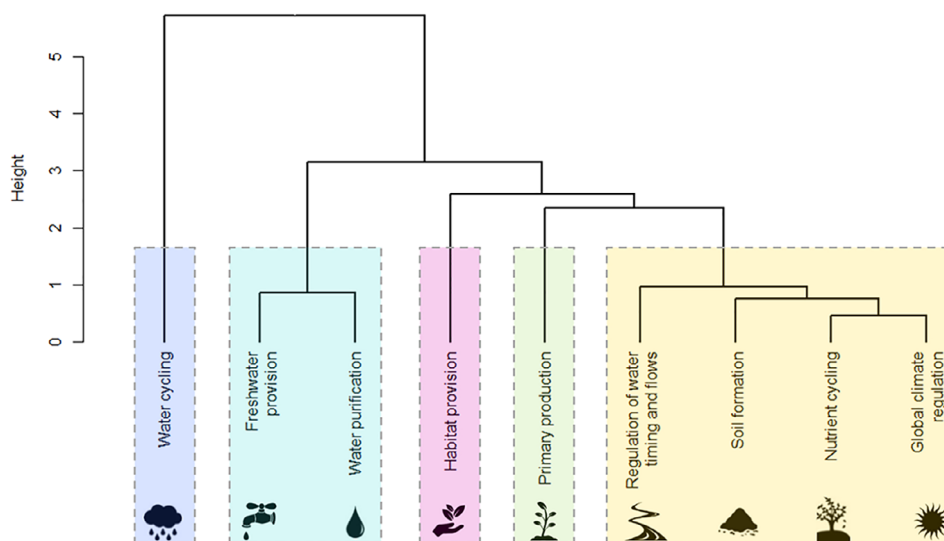


Fig 1. Hierarchical clustering of ecosystem services (ESs). Services within the same box form a cluster (as determined by k-means cluster analysis) and are therefore supplied similarly across eight land covers (low-producing grassland, tall tussock grassland, high-producing exotic grassland, short-rotation cropland, indigenous forest, exotic forest, harvested forest and orchard, vineyard & other perennial crops). A greater separation between the branching points for clusters along the height axis indicates greater dissimilarity among clusters in the extent to which they are supplied by the eight land covers included in this analysis.

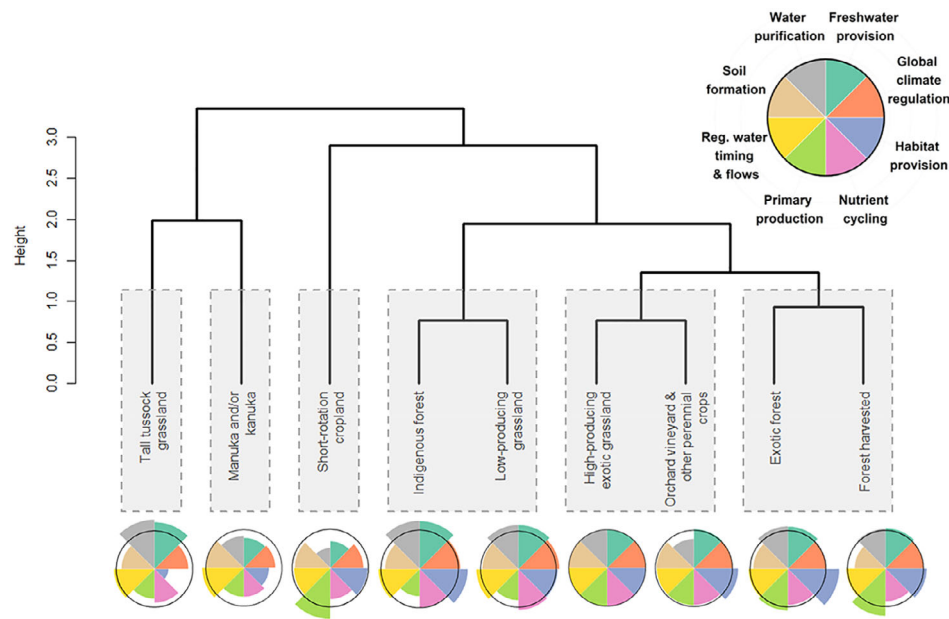


Fig 2. Hierarchical clustering of land covers. Boxes enclose land covers that exhibit a greater similarity in their supply of eight ecosystem services (ESs) (habitat provision, primary production, freshwater provision, soil formation, nutrient cycling, water purification, global climate regulation and regulation of water timing and flows). By contrast, land covers that merge at a greater height have a greater dissimilarity in their service supply. The flower diagrams at the bottom illustrate how each land cover supplies each of the eight ESs, with longer petals indicating a greater supply of an ES. For comparison, the black ring around each flower diagram marks the supply from high-producing exotic grassland, the land cover used as a reference in our meta-analysis.

levels of water purification and freshwater provision, while mānuka and/or kānuka (a successional land cover) is noted for soil formation and regulation of water timing and flows; short-rotation cropland ranks high in supplying primary production. By contrast, the three clusters with pairs of land covers in Fig. 2 exhibit a more uniform supply of the different ESs. Nevertheless, each of these three clusters also appears to supply a distinct ES bundle. The cluster formed by exotic and harvested forests supplies a bundle with high primary production and habitat provision while the cluster formed by indigenous forest and low-producing grassland supplies a bundle specializing in purifying, providing and regulating the flow of water. Lastly, the cluster formed by high-producing exotic grassland and orchard, vineyard & other perennial crops appears to supply even (yet not necessarily high) levels of all ESs.

Greater differences in ES supply can be inferred from the differences in the height at which clusters separate from each other (Fig. 2). Consequently, in Fig. 2, the clusters with two production land covers (harvested and exotic forest plus high-producing exotic grassland and orchard, vineyard & other perennial crops) are similar in their supply of ESs but differ from the cluster with indigenous forest and low-producing grassland. In turn, these three clusters with pairs of land covers are more similar to each other (indicated by the lower branch point) than they are to the clusters with single land covers. The clusters with pairs of land covers are also closer to the short-rotation cropland than to tall tussock grassland and mānuka and/or kānuka, which are more

similar to each other than they are to the rest of the land covers.

The trade-off in service supply between production and non-production land covers was statistically significant [PERMANOVA, Pseudo $F_{1,6} = 3.064$, partial $R^2 = 0.312$, $P = 0.015$ (partial effect of production, when entered before forest cover in a model where variance is attributed sequentially) and Pseudo $F_{1,6} = 3.119$, partial $R^2 = 0.318$, $P = 0.055$ (partial effect of production, when entered after forest cover in a model where variance is attributed sequentially); detailed results in Supplementary Results S4]. The assumption of homogeneous dispersion between both groups was met ($F_{1,8} = 0.718$, $P > 0.05$), suggesting that neither supplies a greater range of ESs among its different land covers. Conversely, the separation between forested and non-forested land covers did not significantly explain the distribution of land covers in ES space [Pseudo $F_{1,6} = 0.536$, partial $R^2 = 0.055$, $P > 0.05$ (partial effect of forest cover, when entered before production in a model where variance is attributed sequentially) and Pseudo $F_{1,6} = 0.592$, partial $R^2 = 0.060$, $P > 0.05$ (partial effect of forest cover, when entered after production in a model where variance is attributed sequentially); see also Supplementary Results S4] nor did the interaction between forested/non-forested and production/non-production [Pseudo $F_{1,6} = 1.159$, partial $R^2 = 0.118$, $P > 0.05$ (both when production is entered before forest cover and when forest cover is entered before production in models where variance is attributed sequentially); Supplementary Results S4].

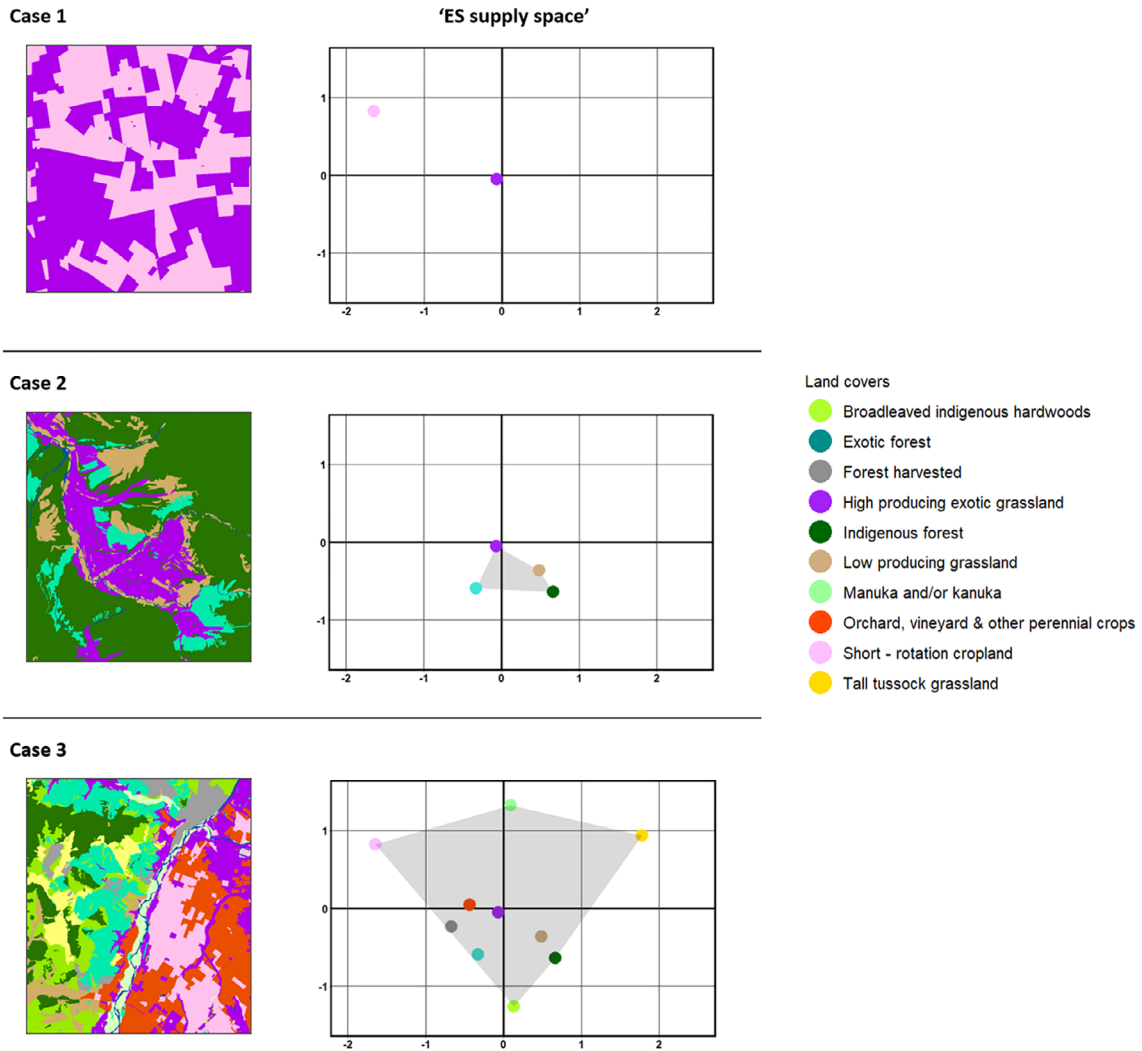


Fig 3. Example visualizations for exploring land cover trade-offs in the supply of multiple ecosystem services (ESs) from entire landscapes. Quantitative measures of ES supply by different land uses or land covers (such as those obtained from our meta-analysis) can be used to generate ordinations that ‘map’ land covers or land uses into the multidimensional space of ES supply (ordination graphs). Distribution of land covers within that space can assist with identification of redundancies in ES supply (among land covers/uses that map close together) and trade-offs among land covers/uses that supply contrasting sets of ESs and, consequently, occupy opposite extremes of the ordination space. Furthermore, the hypervolume enclosed by the total set of land covers/uses from a given landscape expresses the diversity of ESs provided by that landscape. As an example, our data can be used to compare multi-service provision for: a landscape with few, undifferentiated production land covers (Case 1); a landscape with a combination of some production and non-production land covers (Case 2) and a landscape with a broad range of production and non-production land covers that supply a diverse range of services (Case 3).

IV. DISCUSSION

We have synthesized over 40 years of quantitative primary evidence on the ESs supplied by different land cover types at a national scale, and used this to identify bundles and trade-offs among ESs, as well as general land cover characteristics driving these associations. Our method for using existing data to assess bundles, trade-offs and synergies in ES supply across land covers can be used to facilitate the comparison of entire landscapes, for example, by projecting

land covers or land uses into multidimensional ES-supply space (Fig. 3). This mapping could reveal two key characteristics for land-use planning: (i) land covers/uses that cluster together (see also Fig. 2), and thus exhibit redundancy (and potentially resilience) in ES supply, or (ii) land covers/uses that occur at opposite extremes of ES-supply space, and are therefore likely to exhibit complementary roles in their service supply (as ESs are traded off between them). To facilitate the latter, we identified general characteristics that separate groups of land covers in ES-supply space.

We found strong evidence that high-value production land covers supplied a different set of non-market services than all the land covers with low or no production and native elements in their vegetation cover. Together, land covers with low or no production outperformed the production ones in supplying several supporting and regulating ESs (e.g. freshwater provision, disease mitigation and regulation of water timing and flows). By contrast, most production land covers specialized in supplying primary production. The trade-off between water cycling and regulation of water timing and flows (Fig. 1) probably occurred because land covers that allow for increased runoff and present low water retention (such as harvested forests, croplands and built-up areas) deliver more of the water cycling service than land covers that promote soil water storage and, consequently, perform better in regulating water timing and flows (e.g. broadleaved indigenous hardwoods, indigenous forests and low-producing grasslands).

In contrast to the dissimilarity between production *versus* non-production/native land covers, forest cover (either native or exotic) was not associated with significant differences in the suite of services supplied. Instead, we observed a close affinity between land covers with contrasting forest covers (e.g. between low-producing grassland and indigenous forest and between exotic forests and high-producing exotic grasslands) in their supply of several ESs including water purification and regulation of water and timing of flows. Only for habitat provision did we observe that land covers with a forest cover (indigenous forest and exotic forest, both harvested and unharvested) performed better than those without a forest cover in service supply.

Beyond identifying trade-offs among specific land covers, the total hyper-volume occupied by all land covers/uses in the multidimensional ES-supply space (ordination plots in Fig. 3) can indicate the diversity of ESs supplied by all land covers/uses within a given landscape (analogous to interpretations of species in trait space; Laliberté & Legendre, 2010), which could be used in comparisons of existing landscapes or future scenarios.

For example, Case 3 in Fig. 3 has the greatest diversity of land covers and thus occupies the greatest hyper-volume in multidimensional ES-supply space (signifying diverse ES supply). However, there are few land covers at the edge of this volume, such that the full array of services has low redundancy compared with Case 2, where land covers cluster around one location in ES-supply space. Given that resilience in ES supply hinges on the redundancy of the ecosystems supplying those services (Biggs *et al.*, 2012), we would expect that Case 2, with fewer land covers than Case 3 but a greater extent of land covers supplying each ES, would offer greater overall resilience in ES supply than would Case 3, which has a greater diversity of ESs but low redundancy. Because the entire ES-supply space may include areas that do not correspond to any configuration of ESs, this approach is best applied to comparisons of landscapes rather than as an absolute measure of ESs in one location.

Finally, mapping ESs in multidimensional land-cover or land-use space (e.g. Fig. 1) allows the identification of ES

bundles that respond similarly to land cover/land use. These bundles can then be used to identify management decisions that minimize disruption of service flows. For example, ESs related to the soil subsystem clustered together (e.g. global climate regulation was closely linked to nutrient cycling; Fig. 1), likely due to several indicators being shared by both (Supplementary Data Set S4). There was also a gap in our database with respect to the contribution of vegetation and livestock to greenhouse gas fluxes because, in New Zealand, these contributions are well studied *within* a given land cover, but the lack of comparisons *across* land covers/uses limited our ability to quantify changes in this service.

In New Zealand, production land covers are dominant, with exotic forests, high-producing exotic grasslands, croplands, and orchards/vineyards occupying 42% of the country's terrestrial area in 2012 (Landcare Research, 2015). Our assessment, like other ES assessments elsewhere (Costanza *et al.*, 2014), shows that decisions on ecosystem management (such as those leading to the dominance of production land covers) reflect prioritization of a set of ESs over others. Specifically, the trade-offs we find between production and low- or no-production land covers illustrate how the preference for ESs with a high market value and short-term returns occurs at the expense of ESs that have no market value but are essential for sustained, long-term human well-being (Rodríguez-Loínez, Alday & Onaindia, 2015).

The above findings resonate with the recommendations of Foley *et al.* (2011) with respect to halting indiscriminate expansion of agriculture into sensitive ecosystems. However, our findings also suggest that, at the landscape scale, the trade-offs between the ESs supplied by production and non-production land covers can not be solved with a single land cover. Even for the ESs that were best delivered by land covers with no production, we did not find evidence of a single land cover consistently performing better than the rest in the supply of all ESs. Therefore, a landscape with a mosaic of these land covers is more likely to offer a broader suite of ESs than one dominated by large extents of any single low- or no-production land cover (Fischer, Lindenmayer & Manning, 2006; Law *et al.*, 2015).

Thus, we support earlier recommendations to extend beyond the dichotomy of conservation *versus* production land into a more a comprehensive management (Tscharnkte *et al.*, 2005; Grau, Kuemmerle & Macchi, 2013). Such management could, for example, contemplate the extension or restoration of under-represented native land uses at strategic sites where intensive use is not matched by increased production yield, to promote the supply of critical ESs or broaden the existing suite. To this end, management will need to be informed by a comprehensive understanding of how ESs can scale up from individual land-use units and how the relative sizes of different land-use units within a landscape can affect ES supply.

Our analysis shows that low-intensity production land covers that retain some native vegetation (i.e. the low-producing grasslands in our data set) can approach native land covers (indigenous forests) in terms of overall ES supply. These low-intensity

production land covers demonstrate that production and a suite of other ESs can be jointly delivered, providing empirical support to the notion of managed ecosystems with 'restored' ESs proposed by Foley *et al.* (2005). Importantly, we identified great variability in how land covers supplied certain ESs, despite there being high replication in our evidence base for these effects (e.g. erosion control by high-producing exotic grasslands, indigenous and exotic forests). This suggests that local environmental conditions (e.g. slope) and management practices can significantly alter how a given land use affects ES supply (Felipe-Lucia *et al.*, 2018). In turn, this implies some potential to improve ES supply by adjusting management practices within specific land uses (Guerra & Pinto-Correia, 2016; Pang *et al.*, 2017) or incorporating local environmental conditions better into land-use decisions. Within individual land uses, decisions on which practices to adopt will require detailed research on the effects of different management regimes on ES supply (Guerra & Pinto-Correia, 2016; Maseyk, Dominati & Mackay, 2018), as well as an understanding of the extent to which the plasticity in ES supply is constrained (or favoured) by environmental factors.

A critical challenge in applying the ESs framework to spatial and environmental planning is understanding the extent to which different land uses affect ES supply (Braat & de Groot, 2012). The uneven coverage of different ESs that we observed in the literature reflects both variation in the difficulty of quantifying the supply for different ESs and the likely relevance of comparing the supply of certain ESs among land uses. Within our data set, supporting and regulating ESs are best represented. In the global literature, regulating ESs are also the most commonly quantified and mapped category, however, they are usually followed by provisioning ESs, while the evidence on supporting ESs is scarce (Martínez-Harms & Balvanera, 2012; Crossman *et al.*, 2013; Howe *et al.*, 2014; Malinga *et al.*, 2015). The limited representation of provisioning ESs in our data set possibly occurred because most provisioning ESs (e.g. milk, timber) are linked to single or a few land covers and, consequently, are unlikely to be compared across land covers. Such services, however, enter the market directly and can be quantified more readily in monetary terms. By contrast, the supporting and regulating ESs that predominate in our data set usually translate to externalities in the context of production systems, and are more likely to be quantified through biophysical indicators than monetary units (Howe *et al.*, 2014; Czúcz *et al.*, 2018).

Cultural ESs are poorly represented in our database, with the few indicators for this category all being shared with the capture fisheries provisioning service, because they pertain to eels, which are of cultural significance to Māori in New Zealand. Cultural ESs encompass a diverse set of services and have non-material and ideological dimensions that are not readily quantified. The comprehensive methodologies and frameworks that have recently been introduced to quantify the supply of cultural ESs include the use of cultural texts and materials (e.g. paintings, songs, literary texts) as evidence for these services (Cabana *et al.*, 2020). Future ES assessments may therefore benefit from combining our approach (based on quantitative evidence) with these recent

developments focusing on the evidence in cultural materials and representations. In addition, aesthetic value (which is a subset of cultural ESs) may be captured by differences in land values, although land value (for example of a farm) may be influenced by adjacent land covers, rather than pertaining to the land cover that provides the service (e.g. a natural area). Such impacts would be difficult to capture with land cover comparisons like those we used, although they present an interesting avenue for future landscape-scale comparisons. Because the cultural ESs we quantified were specific to species known to be harvested by Māori, and to the scale of single land covers, we caution against extrapolating these findings (Fig. S36) to cultural ESs in other contexts such as recreation and aesthetics.

More generally, it has been suggested that many cultural ESs (e.g. ethical, spiritual, and inspirational values) escape the instrumental value domain present in the ESs framework. Instead, they fall under the relational domain, whereby value is not solely defined in terms of the direct benefits derived from an ecosystem, but also in terms of the social webs of desired and actual relationships constructed around that ecosystem or its components (Chan *et al.*, 2016). However, the domain of relational values is not limited to cultural ESs and can also be found in the sense of stewardship, identity belonging and moral responsibility that people uphold when thinking of regulation, provisioning and supporting services. Consequently, a quantitative approach like ours should be complemented with assessments that address the relational dimensions of the values people hold for the natural elements and ESs in different land uses, to represent their importance better across multiple value domains (Lyver *et al.*, 2017).

Individual ESs are defined to encompass distinct processes and values, but these are often quantified by overlapping sets of indicators (Czúcz *et al.*, 2018). For example, in our data set indicators from water and soil pertained to more than one ES (e.g. water purification and provision of fresh water both share indicators of water quality, while erosion control and soil formation share indicators on soil stability). ES indicators can also occupy different positions in the spectrum connecting the supply and demand ends of ESs (Villamagna, Angermeier & Bennett, 2013). Here we have focused exclusively on the supply end and, more specifically, on the capacity of land covers to provide ESs rather than on their actual flow or delivery as benefits perceived by a specific group of individuals.

Since the Millennium Ecosystem Assessment was released, there have been initiatives to redefine ESs and their categories (TEEB, 2010; CICES, 2018). Here we argue that future work in determining how best to quantify ESs, their potential and realized delivery, and their spatio-temporal variation, will be at least as important as refining their taxonomy. Furthermore, if a focus on quantifying ESs reveals aspects of services that are best left unquantified (such as the relational domain of cultural ESs), this could also lead to the development of alternative ways of assessing those ESs, which could then be applied in combination with quantitative approaches like that developed here. Recent developments, like the

concept of nature's contributions to people and the framework for their assessment proposed by Díaz *et al.* (2018), provide an opportunity for reconciling these issues.

Our work illustrates how existing data can be used to assess bundles and interactions across multiple ESs and land covers in a more cost-efficient way than through direct field observations of each service on each land cover. We also provide evidence of the land-cover characteristics driving ES associations across all the land covers in a temperate country. Yet, an important caveat to our approach stems from underlying factors that are correlated with land use and impact the supply of certain ESs. For example, since land uses such as forestry and natural habitats are frequently found on steep slopes, this physical characteristic will likely influence erosion control in a way that covaries with land cover. At the most extreme end, some ESs may not be related to land cover, but rather respond to other spatially variable factors (e.g. aesthetic values from housing location on hillsides). These factors were beyond the scope of our work, as we did not separate the effects of spatial factors from those of land cover. In fact, one could argue that land use is not selected independently from the local environment, so these factors are a frequent (although not universal) component of any land use and its influence on ESs. Future approaches may benefit from examining how these factors affect the between- or within-land-use differences in ES supply.

This distinction would allow a shift from comparisons across locations (as examined here), which allow comparisons of the components of existing landscapes, to the predicted impacts of land-use change on ESs at any location. However, such predictions would also need to incorporate legacy effects of past land uses, as these can have enduring consequences on ecosystem functioning (Dallimer *et al.*, 2015; Perring *et al.*, 2016). Similarly, for such predictions, it would be important to consider the effect of the configuration of land-use types within a landscape (see above discussion regarding aesthetic services), as this has also been shown to be an important complement to the composition (and diversity) of land covers in determining ESs (Obiang Ndong *et al.*, 2020) and their resilience (Loreau *et al.*, 2003; Biggs *et al.*, 2012). Thus, there are many potential avenues to extend our approach, which opens the way for incorporating existing sources of information actively into ESs research and informing practitioners to shape land systems that sustainably support human well-being.

V. CONCLUSIONS

- (1) Our synthesis of land cover supply of ESs in New Zealand revealed a consistent trade-off in the services supplied by high-value production land covers *versus* those with low or no production and native elements in their vegetation cover. While production land covers specialized in the supply of primary production, low- or no-production land covers supplied a broad array of supporting and regulating ESs. We did not

find any evidence that forest cover was associated with any distinct patterns of ES supply.

- (2) We show that the trade-off between ESs supplied by production and non-production land covers can not be solved with a single land cover. In contrast to earlier suggestions that a single natural ecosystem can support multiple ESs at high levels (Foley *et al.*, 2005), our analyses reveal that a mosaic of different land covers will be required to supply multiple ESs within a landscape.
- (3) We show that exploring how different land covers map on to multi-dimensional ES space allows for an assessment of how diverse and resilient different combinations of land covers can be in their supply of ESs. Such assessments can effectively support land-use planning decisions beyond considerations of the specific identity of each land cover and the ESs it supplies.
- (4) We demonstrate how existing data can be used to assess ES bundles and, in so doing, reveal a method that is more cost-efficient than direct field observations for incorporating fine-scale detail into comprehensive, nationwide assessments of ES supply across multiple land covers. However, we also find that effective landscape management of ESs will require further research on how environmental and land-management factors can mediate the effects of land use on ES supply, and how spatial patterning determines cross-habitat service supply. We anticipate that these effects will differ across ESs and will be more pronounced for ESs where there is high variability in supply by individual land covers (e.g. erosion control in our data set).

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VII. REFERENCES

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VIII. Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Supplementary Methods S1. Detailed data collection and processing methods.

Supplementary Methods S2. Full search phrase for pilot and formal searches.

Supplementary Methods S3. Decision tree with selection criteria used in the full-text assessment of publications with relevant abstracts for our review.

Supplementary Methods S4. Conversion of confidence intervals to variance and imputation of missing values.

Supplementary Methods S5. Scree plots and land cover classification for multivariate analyses.

Supplementary Results S1. Overview of research effort for New Zealand.

Supplementary Results S2. Evidence base and network meta-analysis for individual ESs.

Supplementary Results S3. Summary of log response ratios per land cover and ecosystem service combination.

Supplementary Results S4. Detailed results from PER-MANOVA analyses.

Supplementary Results S5. Data analysis with allocation of a single ES to each indicator.

Supplementary Data Set S1. Overview of Ecosystem Services (ESs).

Supplementary Data Set S2. Overview of land cover classes as defined in New Zealand's Land Cover Database (LCDB) (Thompson *et al.*, 2003).

Supplementary Data Set S3. Reference list for the studies included in our meta-analysis.

Supplementary Data Set S4. Quantitative indicators used to quantify supply of each ecosystem service.

Supplementary Data Set S5. Final log response ratios on ecosystem service supply for pairwise comparison of land covers in each study used in our analysis.

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